HYBRIDIZATION OF WILD PLANTS

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(WITH FOUR FIGURES)

THE number of forms of plants which have been or are regarded as hybrids by systematists is a large one and includes several oaks, of which two have been examined during the last two seasons. Attention has been called previously to the untrustworthiness of the custom prevalent among botanists of attributing a hybrid origin to certain plants because they appear to exhibit halved, fused characters, or a mosaic of qualities derived from the two suppositious ancestors. In some instances such deductions have been made by which the ancestry of a questionable plant has been made to include three or even four species. The argument of distribution is the main one offered in such attempted demonstrations. In many cases, this together with other circumstantial evidence may amount to almost positive conviction, but unless this close relation of well-joined facts is furnished, assertions as to the hybridity of a plant must be taken simply as a suggestion to be tested by cultural or experimental methods.

When confronted with an enigmatical plant of such character, three methods of attack are available to the investigator: that of obtaining the supposed hybrid by synthetizing it from its supposed parents; that of making an anatomical examination of the hybrid and the parents to which it has been referred; and that of obtaining second, third, and succeeding generations of the hybrid for the purpose of ascertaining whether or not any separation of the ancestral characters may occur in an alternative inheritance by which the ancestral forms may actually reappear. All of these methods are beset with numerous difficulties, but when used together with the facts of distribution a very satisfactory degree of proof may be obtained. It will be profitable to consider the scope and application of the various methods of experimentation and observation noted above.

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The re-formation of a hybrid by the cross-pollination of the parents to which it may be ascribed is by no means simple in all instances, nor is it always easy of accomplishment. In the first place, the original cross-pollination may have taken place possibly under an exceedingly rare combination of favorable physiological conditions difficult to secure or duplicate in experimentation. Then one or both of the species as ordinarily recognized may in reality consist of two or more elementary species, which may not differ widely in external anatomical characteristics, but exhibit widely divergent physiological characters and behave quite differently in breeding. A hybrid with one of these forms may differ in very many important particulars from a hybrid with another constituent of the same species. Of course if we deal with elementary species only in our usage of the term, this difficulty does not exist; but it does appear as a serious matter with the customary practice, as has been found in a number of breeding experiments, and furthermore must be taken into account no matter by what method we consider a hybrid.

Let us suppose, however, that we have actually in hand the two strains or elementary species by which the hybrid may have arisen, and we have still one more matter which may mislead us. This consists in the fact that reciprocal crosses are not always identical in their products. Thus the pollen of *A* and the egg of *B* do not necessarily make the same hybrid as the egg of *A* and the pollen of *B*.

The pollination of *Oenothera Lamarckiana* by *O. biennis* generally results in securing a progeny separable into seven types, some of which are stable and reproduce themselves exactly in succeeding generations, while others split into two or more forms in the second generation. On the other hand, the use of pollen of *O. Lamarckiana* on pistils of *O. biennis* results in a progeny embracing four types, none of which is identical with the components of the reciprocal cross. *O. biennis* shows a similar behavior in some other crosses in the limited observations recorded. In all such cases it must be understood that the number of types does not appear to be invariable, and that a progeny of a hundred thousand is likely to include more than one of a score. It is evident that in the determination of a hybrid by this method difficulties may be met with. Thus the failure of the operator to secure the supposed hybrid may not be considered

as final proof that it may really have come by one of the rarer combinations which he has missed. On the other hand, success may come with the first cross and in the first generation.

In some instances the result of a hybridization is a single type which offers the qualities of the parents locked in a stable combination in the first generation and reproducing without separation in successive generations. It is this type of hybridization that is implied in the general assertions as to the hybrid origin of any plant, and it is a type of which we have the fewest illustrations in breeding experiments. To recur again to the genus furnishing the example previously given, *O. cruciata varia* was suspected by the author to be a combination of *O. Lamarckiana* and *O. cruciata*, and in the synthetization test the good fortune was encountered of selecting the one of the three known elementary species of *O. cruciata* which had originally entered into the union. The egg of *O. Lamarckiana* and the pollen elements of this form entered into a stable combination which has the distinctness and fixity of a species, and as a matter of fact this hybrid has been long mistaken for the true *O. cruciata* by a great number of European gardeners and botanists.

In addition to the difficulties of hybridization and interpretation of the results described above, it is also to be taken into account that in some instances a long period ensues between the act of pollination and the perfection of the fruit, and then a long time is necessary for the germination of the seeds and development of the progeny. Ten, fifteen, or even twenty years might be necessary to make an application of this method to some of the species of trees, which would obviously make it unavailable except under extraordinary circumstances.

The examination of the anatomical characters of a plant to determine its ancestry is a method which has become of less esteem in the light of modern additions to information as to the character and behavior of hybrids. Of the various types of hybrids described it is of course the fixed hybrid which is most likely to come under examination, and while it occasionally presents a fair average of the characters of the parent, more frequently it is goneoclinic to one or the other, and may be so near one parent that a gross or minute estimate of the tissue structure would offer nothing better than a guess as to the

other parent, a guess which might be fortified to some extent, perhaps, by the facts of distribution. In certain meristic qualities, such as the rate and total amount of growth, the hybrid may even exceed that of either parent, or be less than either.

The mistaken impression prevails that hybrids bear defective pollen, but this is generally found to be the case only when the cross is unbalanced in many characters, particularly those appertaining to the reproductive functions. The infertility of many animal hybrids has also strengthened the assumption that plant hybrids share this defect. Many hybrids are quite as prolific in mature seeds as either parent, while in some that are offered by the seedsman and nurseryman they are claimed to excel in this respect.

In any case where the comparative anatomical method is used, care must be taken to make observations upon material from similar stages of development. This is forcibly impressed upon one after following the growth of a hybrid which in the seedling stages shows a predominance of the qualities and anatomical characters of one parent, a different arrangement in the adult shoot, and a still different balance in the flower and fruit.

The third method of study of a supposed hybrid is one which involves pure cultures of its progeny for one or two generations. If it should be a fixed hybrid no results will be secured which will be of value in the solution of the problem, since, so far as any facts offered by such cultures are concerned, the plant behaves as any other species. Presumably most of the species of suspected hybrid origin are of this character, but some of them undoubtedly will be found to be constantly re-formed and to offer alternative inheritance, and hence this test should be applied whenever practicable.

If the supposed parents differ in but one or a few characters, and the hybrid shows alternative inheritance, the solution of the main question lies near at hand. It is not such simple questions as this however that we are usually called upon to solve. The real difficulties lie in the hybrids with the component qualities in stable combination, making a fixed hybrid, and with the forms which exhibit an interlocked combination of the ancestral characters in the first generation which resolve into the possible combinations of the dissimilar characters in the second, by which an enormous range of indi-

viduals is presented, which without close examination of a large progeny might appear to be a hopeless medley. This is best illustrated by a plant which has been studied recently in cultures at the

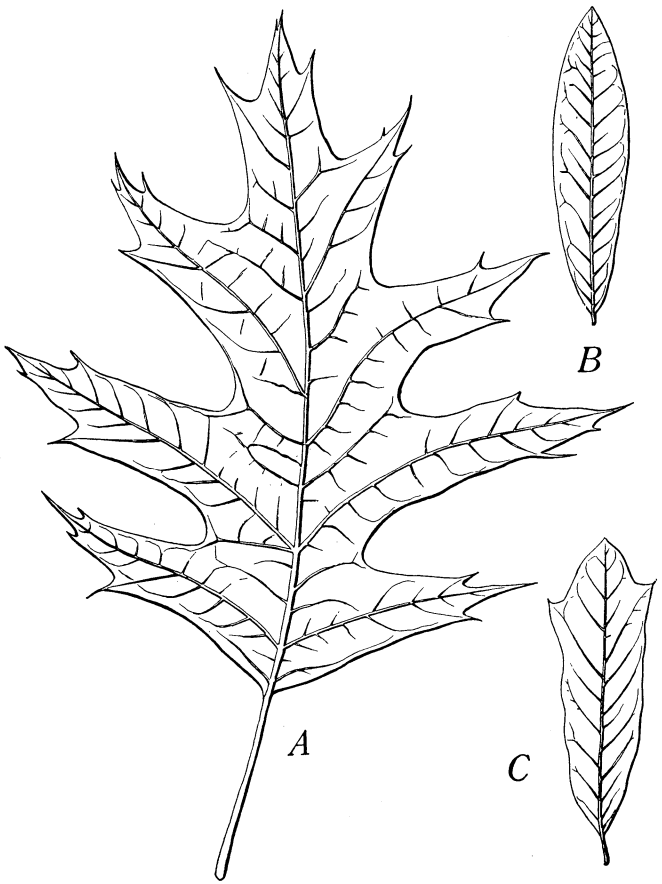

FIG. 1.—*A*, leaf of *Quercus rubra* from N. Y. Botanical Garden; *B*, leaf of *Q. Phellos* collected at Ashland, N. J., Sept. 14, 1892; *C*, leaf of *Q. heterophylla* taken from tree from which acorns were taken for cultures, collected at Richmond Valley, Staten Island, N. Y., October 22, 1905.—×½.

New York Botanical Garden, and at the Desert Laboratory, Bartram's oak, *Quercus heterophylla*.

Bartram's oak was discovered as a single individual growing on a farm of Mr. John Bartram, near Philadelphia, on the banks of

the Schuylkill at some time previous to 1750. A rather complete history of the occurrence of other individuals which were included with this tree under the name of *Q. heterophylla* is given by Dr. ARTHUR HOLLICK in *Bull. Torr. Bot. Club* (**15**:303. 1888) and need not be repeated here.

After a consideration of various lots of material which appeared to differ widely, various botanists have regarded this tree as a hybrid between *Q. Phellos* and *Q. tinctoria*, *Q. Phellos* and *Q. falcata*, *Q. Phellos* and *Q. coccinea*, *Q. Phellos* and *Q. palustris;* while others have designated it as a variety of *Q. Phellos*, *Q. coccinea*, *Q. aquatica*, *Q. nigra*, and *Q. imbricaria*. It is notable that of the botanists who ascribed a hybrid origin to the plant all agreed that *Q. Phellos* must be one of the parents, a fact which will be easily explainable when an examination of its leaves is made.

In October 1905 the author was accompanied to a locality on Staten Island by Dr. HOLLICK and Dr. BRITTON, where several trees of the species had been under observation by them for many years. About 75 acorns were procured from a tree which bore leaves of a form approximating that of *figs. 2* and *3*, and were placed in the propagating houses of the New York Botanical Garden, with the result that 55 plantlets were available for study in December and January following. With the formation of the earliest leaves it became evident that a wide diversity of form of these organs and of other qualities prevailed, as shown by the photograph taken in April.

In May 1906 all of the plantlets were transferred to the experimental grounds, and as development proceeded the diversity became still more marked. At the close of the season it could be seen that this group of plants included some which simulated *Q. Phellos* with its lanceolate entire leaves, while others were not separable from *Q. rubra*, the remainder being capable of arrangement in a series between these two poles. An examination of the literature disclosed the fact that the combined observations of the several botanists who have written on the subject refer to plants bearing almost the entire range of leaves noted in the cultures here described. In most of these accounts the leaves are said to be much like those of *Q. Phellos*, while some observations include notices of others which were broad lobed and notched, although most of these writers were extremely chary of

identifying any of the forms with those of *Q. rubra*. It is to be noted, however, that as a result of the consideration of gross anatomical facts and distributional data, Dr. HOLLICK and other botanists had finally concurred in the general conclusion that the tree was in all probability a hybrid between the red oak and the willow oak.

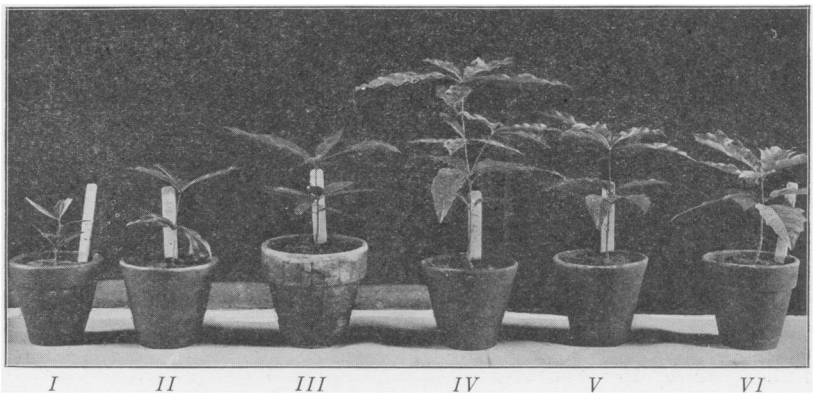

FIG. 2.—Plantlets from progeny of tree of *Q. heterophylla* which bore leaves as in *fig. 1, C*. *I* bears leaves not distinguishable from those of *Q. Phellos*, and *VI* resembles *Q. rubra*. *II*, *III*, *IV*, and *V* form a series between *I* and *VI*.—Photographed April 1906.

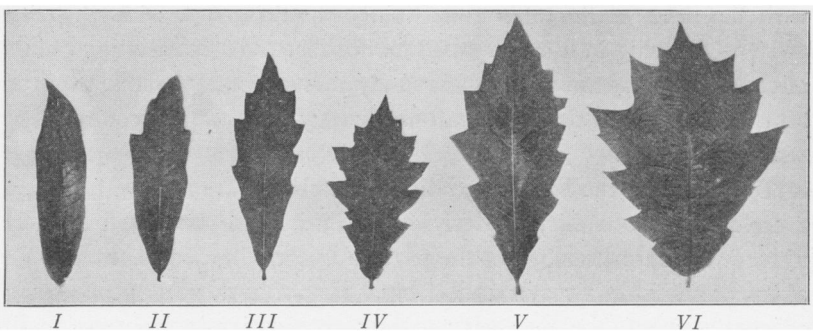

FIG. 3.—Series of leaves from progeny of *Q. heterophylla*, parallel to those shown in *fig. 2*, but taken at the close of the season of 1906.

With our present available information concerning the behavior of hybrids this conclusion seems unavoidable. If we attempt to follow out the history of the hybridization as it may have occurred, however, we are compelled to rely upon inference in part. The

actual nature of the immediate product of the cross is not known. The parental species have undoubtedly sustained similar distributional relations to each other for uncounted hundreds or thousands of years, and there is no reason to suppose that hybridization may not have taken place many generations ago. On this account it is not possible to say whether the tree from which the germinated acorns were taken was the immediate product of the cross or whether it is the *n*th generation of its progeny.

In balanced crosses in which the parents show a large number of dissimilar characters, the first generation rarely offers the spectacle of pure dominance of the characters derived from one parent, and recessiveness of those from the other parent. It is only when the parents differ by a point or two only that such total dominance is seen, and the first generation or the immediate product of the cross resembles one parent or the other, and its progeny split in the next generation. In cases such as that under discussion, and which is also illustrated by the walnuts, the first generation shows a mixed dominance as well as a possible fractionization of some meristic qualities, so that the hybrid appears as an intermediate between the two parents, toward both of which its relative position may be variously estimated. In the second generation the movements of the recessives coupled with the range of fluctuating variability should give a wide diversity of types, varying in number with the number of differentiating points of the parents of the cross, which may include both parents, the type of the first generation, and an intricately interwoven connecting series of forms.

By reason of the number of dissimilar characters involved in such a cross, the probability of deriving an individual composed entirely of recessive characters, or of the particular combination characteristic of either ancestor is very small. A progeny of hundreds of thousands of species would be necessary to furnish a series inclusive of both ancestors and intermediate combinations.

While it may not be said that any of the plantlets of the progeny under observation are reconstituted ancestral forms, yet some of the individuals include so many of the qualities of the red oak and willow oak that the evidence is overwhelmingly in favor of the conclusion that the origin of *Q. heterophylla* is to be attributed to the hybridiza-

tion of these two forms. Taking this conclusion as established, it may then be said that the name *Q. heterophylla* is at present applied to a medley of oak trees which possibly includes the first generation of a cross between *Q. rubra* and *Q. Phellos*, secondary hybrids with either parent, as well as successive generations in which various combinations of ancestral qualities may appear.

Another aspect of the parental form of the above hybrid and the progeny remains to be mentioned. A collector covering the field occupied by the hybrid in which the parental forms come into contact, who gathered a full series of material from the trees available, would have data upon which mistaken conclusions as to intergradation of species by fluctuating variability might be made. This leads to the suggestion that any supposed intergradation of two species of seed-plants should be examined with respect to possible hybridizations before any final estimate is reached in the matter.

Furthermore, it is to be seen that while in all reasonable probability opportunity for hybridization between these two oaks has been present for a period of unknown but undoubted great length, it has not resulted in anything in the way of occurrence or distribution suggestive of the disappearance of either parental form. The probably greater frequency of intra-specific fertilization over hybridization would secure this result. Then again it is to be seen that even in the case of complete cross-fertilization of all of the individuals there would be the probable reconstruction of the ancestral forms among the progenies.

Quercus Rudkinii has long been reputed to be a hybrid between *Q. Phellos* and *Q. marylandica*, and a visit was made to the group of trees from which the species was originally described by Dr. BRITTON, in company with him and other botanists in October 1905. These trees stand near Cliffwood, New Jersey, and since the original discovery in 1881 others have been found on Staten Island and also to some distance to the southwestward in New Jersey. The mere facts of distributional relations together with the anatomical features offered by the bark and leaves led to the description of these trees as being of a hybrid origin from the willow oak and the black oak. If these facts only are taken into account, it seems quite as plausible to regard this tree as a hybrid as *Q. heterophylla*. The leaves from the included trees showed a range of forms that included the type

of *Q. Phellos*, but did not go wide enough to show duplicates of those of the other parent as described and figured by Dr. BRITTON (*Bull. Torr. Bot. Club* **9**:13. 1882). The acorns likewise ranged from the form near that of *Q. Phellos* toward *Q. marylandica*, but included none that might be mistaken for the latter. The bark of the various individuals, on the other hand, seemed most like *O. marylandica*, although much variation was apparent (*fig. 4*).

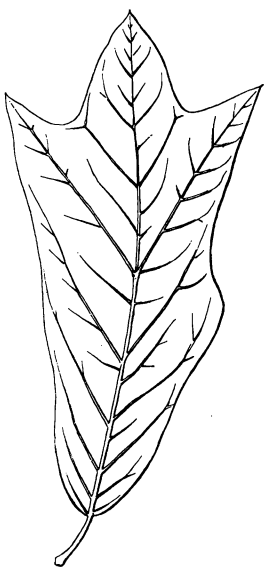

FIG. 4.—Leaf of *Q. Rudkini* taken from tree at Cliffwood, N. J., from which acorns were taken for cultures.—×½.

During the visit of 1905 acorns were found on trees of some of the types only, and material capable of germination was obtained from three of them. When these were at the end of the first year's growth, which began in the propagating houses in January 1906 and ended in September, it was seen that the progenies of the three parents, selected for their dissimilarity, were fairly identical; and while a wide range of variability was found, this range did not exceed the limits of similar fluctuations offered by other species of oaks which are known to be unified hereditary strains.

Over a hundred plantlets were carried through the first season, but no leaf-forms were exhibited which might be taken to simulate either of the supposed ancestors, although a comparative culture of seedlings of these might have brought some resemblances to light. The advanced stages, however, may modify this aspect of the progeny materially. Some of the trees examined bore only imperfect acorns, and the proportions incapable of germination taken from all of the individuals was large. This and other facts suggests a more widely unbalanced cross than in the case of Bartram's oak, and it is quite possible that the dissimilarity may be so great that a finely graded series or a total series may be impossible in the actual combinations effected.

As the facts now stand, however, the observations have not given any actual proof of a hybridization, although in view of the above

considerations this is not disproved. Synthetic tests, which would consume a large fraction of a human life-time, and anatomical examinations are yet to be resorted to. Meanwhile this oak, which seems to be constant in successive generations within the limits of its variability, must be regarded as a species in accordance with current taxonomic practice, until some positive evidence to the contrary is obtained.

The principles illustrated by the foregoing facts may be briefly summarized as follows:

It is obvious that the facts of geographical distribution may be relied upon to furnish conclusive evidence as to the origin of a species or a hereditary quality only under very exceptional conditions, in which other possibilities are excluded, and then only in a circumstantial manner. It is of course a basal and necessary fact that species not in contact may not hybridize, but the converse is true only when otherwise proven.

So far as the plants of suspected hybrid origin from parents suggested by distributional relations are concerned, the methods of investigation available are two, which may separately secure affirmative evidence of conclusive value, while the third may bring no more than confirmations and suggestions.

Attempts at synthetization, if successful, yield dependable conclusions as to the composition of a hybrid, yet a failure to secure a form by synthesis may be due to innate and almost intangible difficulties in the hybridization of the forms concerned, by the different results of reciprocal crossing, and the difference in physiological attributes of elementary species included under one name. Furthermore, the natural form, the ancestry of which is under search, may have been a derived hybrid which became fixed in the *n*th generation by a fortuitous combination of dominant characters. To secure a similar result in an experimental test might be beyond the range of probability.

In an anatomical examination such a combination of dominant and recessive characters with fluctuations in meristic features away beyond either parent may make the results of but little value until confirmed by data derived from other sources, before their full value may be known.

A study of a fixed hybrid by cultural tests of its progeny will reveal

nothing as to its origin, and synthetization and anatomic examinations are the only recourse. On the other hand, if the progeny exhibits alternate inheritance, its components may show unmistakably the nature of the original cross.

The last-named method demonstrates beyond reasonable doubt that Bartram's oak is a hybrid derivative of the willow oak and red oak, the progeny being probably characterized by alternative inheritance of some of the qualities, and fractionization of others, instead of being a unified hereditary strain. Some of the plantlets included in a progeny of 55 individuals were apparent re-constructions of the ancestral types as observed at the close of the first year, while others were variously intermediate.

Rudkin's oak, on the contrary, yields no evidence in cultures of its progeny on which a defensible conclusion as to its origin may be based. The individual variability of the trees included under this name is very great, and some of these approach the willow oak in leaf-form, and some in the character of the acorns. The study of a large number of seedlings from three trees showed the willow oak in leaf-form and some of the characters of the acorns. The study of over a hundred plantlets showed a wide and practically identical range of variation. Alternative inheritance could not be traced. The individuals known under the name of *Q. Rudkini* produce a large proportion of imperfect acorns, but beyond this no facts suggestive of hybrid origin can be found, except the anatomical resemblances noted.

A list of the natural plant hybrids of North America was prepared by Mr. DAVID GEORGE for presentation at the International Hybrid Conference in New York in 1902, but was not published. In this list it was noted that 117 natural hybrids had been reported as occurring in the indigenous flora of North America, in addition to some instances among the ferns and mosses. The manuscript having been placed at my disposal by the director of the New York Botanical Garden, a revision of the list has been made, some of the original references being omitted and a few added. No attempt has been made to make it actually complete, the sole purpose being to suggest material for extended observations similar to those described in this paper. The reported hybrids are distributed among the natural families as follows:

NAIADACEAE.—Two cases in Potamogeton.

CYPERACEAE.—Twelve hybrids in Carex.

JUNCACEAE.—One hybrid between *Juncus effusus* and *J. pacificus*.

LILIACEAE.—One hybrid between *Calochortus Benthami* and *C. albus*.

ORCHIDACEAE.—One hybrid between *Habenaria lacera* and H. *psycodes*.

JUGLANDACEAE.—Three hybrids of *Hicoria pecan* with *H. minima*, *H. alba*, and *H. laciniosa;* one hybrid between *Juglans nigra* and *J. cinerea*.

SALICACEAE.—About twenty supposed hybrids of Salix are noted; two hybrids of Betula are also reported, viz., between *B. pumila* and *B. lenta*, and between *B. populifolia* and *B. papyrifera*.

FAGACEAE.—Thirty-five oak hybrids have been reported, but one of these, *Q. Rudkini*, has been tested, as described above, with negative results.

RANUNCULACEAE.—A hybrid between *Actaea alba* and *A. rubra; Clematis viornoides* is reported to be of a hybrid nature.

CRUCIFERAE.—*Roripa palustris* is supposed to form natural hybrids with *R. obtusa* and *R. sinuata*.

POMACEAE.—*Malus Soulardi* is taken to be a cross between *M. coronarius* and *M. Malus* by some workers.

ROSACEAE.—*Geum strictum* and *G. canadense* are supposed to form a hybrid.

PAPILIONACEAE.—A hybrid between *Baptisia australis* and *B. bracteata* is reported.

ANACARDIACEAE.—*Rhus hirta* is supposed to cross with *R. glabra*.

RHAMNACEAE.—*Ceanothus Lobbianus* is taken to be a hybrid between *C. thyrsiflorus* and *C. dentatus;* it is also supposed that *C. thyrsiflorus* hybridizes with *C. papillosus* and *C. sorediatus*.

VIOLACEAE.—A large number of hybrids of Viola have been reported.

ONAGRACEAE.—*Oenothera biennis* and *O. Oakesiana* hybridize, the progeny of the first generation consisting of several types.

CACTACEAE.—A hybrid is supposed to be formed between *Opuntia fulgida* and *O. spinosior*.

CORNACEAE.—*Cornus Baileyi* has been taken to be a hybrid between *C. asperifolia* and *C. stolonifera*.

VERBENACEAE.—The evidence seems strong that *Verbena canadensis* and *V. bracteosa*, *V. bracteosa* and *V. hastata*, *V. bracteosa* and *V. urticifolia*, *V. bracteosa* and *V. stricta*, *V. stricta* and *V. hastata*, *V. stricta* and *V. urticifolia*, *V. urticifolia* and *V. hastata*, *V. angustifolia* and *V. stricta*, *V. angustifolia* and *V. bracteosa* hybridize.

ACANTHACEAE.—*Ruellia ciliosa parviflora* has been supposed to be the result of a cross between *R. ciliosa* and *R. strepens*.

LOBELIACEAE.—*Lobelia syphilitica* is supposed to hybridize with *L. cardinalis*.

CICHORIACEAE.—*Prenanthes Mainensis* is taken to be a cross between *Nabalus racemosus* and *N. trifoliatus*.

COMPOSITAE.—Hybrids are reported in Eupatorium, Solidago, Aster, Bidens, and Helenium.

The genera noted above are supposed to offer about two hundred hybrids, and as the observations have been made principally with the flora of eastern North America, in a region which probably does not furnish more than four thousand species, it is to be seen that the questions involved affect about 0.5 per cent. of the flora. Probably not more than half of the instances included in the above list could be confirmed by actual tests; but on the other hand a closer examination of other genera would reveal an equal number of actual occurrences.

Some of the constituents of the native flora are known to be constant unitypic hybrids, and hence have every claim to be regarded as species. The type of hybridization most widely different from this is illustrated by Bartram's oak, and between these two diverse modes of action may be found. In gaining a more extended and accurate knowledge of the manner in which the qualities of separate unified strains of plants are alternative, or are interlocked, or fractionized in hybridizations, a vantage ground will be gained for the consideration of all questions in genetics as to saltations, minute accretions, and fluctuations of such characters.

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